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VASICENTRIC TRACHEIDS AS A DROUGHT SURVIVAL  
MECHANISM IN THE WOODY FLORA OF SOUTHERN  
CALIFORNIA AND SIMILAR REGIONS;  
REVIEW OF VASICENTRIC TRACHEIDS

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ABSTRACT

Vasicentric tracheids are defined as tracheids present adjacent to vessels in a wood which also possesses libriform fibers or fiber-tracheids as imperforate tracheary elements. Vascular tracheids would correspond with this definition, but are defined as occurring only in latewood, whereas vasicentric tracheids occur throughout a growth ring or in wood of a diffuse-porous species. Vasicentric tracheids offer a subsidiary conducting system which can supply stems and leaves when the vessels to which vasicentric tracheids are adjacent fail because of air embolisms. True tracheids (present as the sole imperforate tracheary element type in the woods in which they occur) have much the same physiological effect, maximizing potential safety in conduction. Vasicentric tracheids, vascular tracheids, and true tracheids are alike in being imperforate tracheary elements bearing relatively large bordered pits approximately like those on lateral walls of vessels in density. Libriform fibers or fiber-tracheids also occur in woods in which vasicentric tracheids or vascular tracheids are present. Vascular tracheids, by virtue of occurrence only at the end of a growth ring (where they grade into narrow vessel elements), maintain water columns in stems, which thereby persist through dry seasons, but may not adequately supply leaves, which may wilt as drought progresses. Vasicentric tracheids, by safeguarding the conduction of all parts of a growth ring, seem related to the evergreen habit which many shrubs possessing vasicentric tracheids have. Phylads with true tracheids are relatively few in dicotyledons, and only a small part of these groups have evidently succeeded in adapting to dry climates. The numerous phylads which instead have libriform fibers or fiber-tracheids have developed comparable safety by evolving vasicentric tracheids. Therefore genera with vasicentric tracheids bulk large in the floras of areas in which evergreen drought-tolerant shrubs are adaptive, the Mediterranean-type areas of the world. In southern California, 26 families (17 reported for the first time) have vasicentric tracheids; notable genera include *Arctostaphylos*, *Ceanothus*, *Prunus*, *Quercus*, and *Salvia*. Desert shrubs have vasicentric tracheids to a somewhat lesser degree. Other Mediterranean-type areas are surveyed for both vasicentric tracheids and true tracheids. The regions so analyzed are central Chile, southern Australia, the lands adjacent to the Mediterranean Sea, and southern Africa. Genera in these areas with vasicentric tracheids include *Banksia*, *Carissa*, *Eucalyptus*, *Grevillea*, *Hakea*, *Protea*, *Quercus*, *Rosmarinus*, etc. New Zealand and Japan are wetter and have fewer genera with vasicentric tracheids but more with true tracheids. Many drought-tolerant evergreen shrubs have vasicentric tracheids. A new listing of families and genera with vasicentric tracheids is provided for the world flora, with new reports documented and pertinent literature cited. This new listing includes 68 families (33 newly reported in this paper), which represents a considerable advance on the 32 families listed by Metcalfe and Chalk in their compendia of 1950 and 1983, and includes some large and diverse families for the first time (e.g., Ericaceae, Pittosporaceae, Rosaceae). The lack of reports on occurrence of vasicentric tracheids may in part relate to difficulty in identifying these cells; suggestions for analysis are given.

Key words: chaparral, drought resistance, drought tolerance, ecological wood anatomy, tracheids, vascular tracheids, vasicentric tracheids, wood anatomy.

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INTRODUCTION AND HYPOTHESIS

During 1984, I surveyed the woody flora of southern California (as listed in Munz 1974) to ascertain what adaptations with respect to wood anatomy might

be basic to survival of these species under drought conditions. The dry seasons of southern California are unpredictable in length, time of onset, and severity. Some years have very dry winters, and few years approach the mean figures for annual rainfall. Unusual adaptations or combinations of adaptations are to be expected under these conditions, not only with respect to wood anatomy but also with respect to vegetative morphology in general.

During the course of the survey, an unusually high number of genera and species proved to possess vasicentric tracheids. Vasicentric tracheids are not common in dicotyledons at large. Metcalfe and Chalk (1950) list vasicentric tracheids for 32 families. Of these, three should be united (Bonnetiaceae, Guttiferae, and Hypericaceae) as Clusiaceae, and one, Staphyleaceae, seems to lack vasicentric tracheids (Carlquist and Hoekman 1985). Most of the remaining 29 families are small, or contain only one or two genera in which vasicentric tracheids have been reported.

However, the southern California flora proves to have 25 families in which one or more genera have vasicentric tracheids according to this survey. Some of these genera are large, reported as having vasicentric tracheids for the first time, and form conspicuous vegetational elements: *Arctostaphylos* and *Ceanothus*, for example (vasicentric tracheids apparently are present in all species of both genera). Indeed, the typical chaparral genera mostly possess vasicentric tracheids, although this had not been hitherto suspected.

The term "vasicentric tracheid" as used here connotes imperforate tracheary elements, provided with bordered pits about as large and crowded as those on vessel elements. Vasicentric tracheids occur in woods in which libriform fibers or fiber-tracheids also occur, and thus are to be distinguished from what I am calling "true tracheids" for the sake of contrast. True tracheids are found in wood too primitive for evolution of mechanically significant cells (=libriform fibers or fiber-tracheids). Vasicentric tracheids as defined here also differ from vascular tracheids, which are essentially extremely narrow latewood vessel elements which lack perforation plates. Vascular tracheids as defined here occur only in latewood and are not intermixed with wider cells bearing perforation plates. This definition differs only slightly from that of Panshin and de Zeeuw (1980). These authors state that vasicentric tracheids tend to surround vessels whereas vascular tracheids tend to occur in latewood and form vertical series. In my definition, I am omitting the tendency for these elements to form vertical series. In my definition, vasicentric tracheids must, at least in part, be found intermixed with ordinary vessels (and be adjacent to them), whereas vascular tracheids are restricted to latewood (where they form the terminal portion of a growth ring and tend not to be intermixed with vessels). The reason for adopting this definition is that a functional difference is involved and, in fact, different groups prove to have one of the two types of tracheids characteristically, although a few have vascular tracheids so abundant that they enter earlier portions of a growth ring also, and vasicentric tracheids must be said to be present in these portions of growth rings (Asteraceae, Lamiaceae). The definition offered by the IAWA Committee on Nomenclature (1964) is vague and consequently is not followed. Actually, my definitions are, in practice, similar to those of Metcalfe and Chalk (1950); the reader will note that all families claimed by them to have vasicentric tracheids I accept as such also (with the exception of Staphyleaceae). The many families I have added to that list are the result of discovery rather than alteration of definition (except for Cactaceae). My definition of tracheid is that of Bailey

(1936); that definition has been followed by many American workers and some European ones (e.g., Mennega 1980). The distinction Bailey draws between tracheids and fiber-tracheids proves to be a functional one, in that fiber-tracheids and libriform fibers as he defined them do not occur in ways that demonstrate conductive effectiveness, whereas tracheids do seem always to have this connotation, as demonstrated in the present paper and in an earlier one (Carlquist 1984a).

In sum, the central hypothesis based upon this definition and on the observed instances of vasicentric tracheid and vascular tracheid occurrence is as follows. Vasicentric tracheids, by virtue of being adjacent to many of the vessels, safeguard many vessels or vessel groups and can take over the conductive function (at a slow pace) when air embolisms disable vessels. Air embolisms do not disable vessels at times of peak conduction, so a slow rate of conduction as provided by the vasicentric tracheids suffices. The subsidiary conductive function just stated can be expected of true tracheids as well as of vasicentric tracheids. Both vasicentric tracheids and true tracheids permit conduction to continue when vessels are disabled without appreciable three-dimensional rerouting of the conductive pattern. The resistance of tracheids to disabling as compared to vessels is based on the widely held assumption that air bubbles do not cross pit membranes from one tracheid to another, whereas they do spread from one vessel element to another, potentially disabling much of the length of a vessel.

Vascular tracheids can offer safety, but not until the latewood in which they occur has been formed. Vascular tracheids provide water columns which can potentially persist through the dry season, safeguarding the stem but not necessarily its foliage. Foliage might wilt during the dry season in proportion to the number of vessels which had been disabled. During the same period, a plant with vasicentric tracheids would be able to maintain a network of water columns leading to the leaves, which could remain evergreen. Plants with either vascular tracheids or vasicentric tracheids would be advantaged in a Mediterranean-type climate, but the species with vasicentric tracheids might be expected (with exceptions) to be evergreen, whereas species with vascular tracheids might be expected to have drought-deciduous or seasonally deciduous foliage. "Drought-deciduous" is defined here as loss of leaves in relation to loss of soil moisture, whereas "seasonally deciduous" is defined as annual loss of leaves in autumn, regardless of soil moisture. In some woody plants (e.g., *Aesculus*), leaves may be seasonally deciduous in midsummer rather than in autumn.

In areas with a Mediterranean-type climate, evergreen leaves may be hypothesized to have a positive selective value. Rainfall occurs during winter months, so that flower-bud formation, flowering, even fruiting and some growth occurs, based on photosynthesis of existing leaves, before warm weather arrives. This habit can be seen in *Arctostaphylos*, *Ceanothus*, and *Quercus*, as well as in other genera with vasicentric tracheids. Shrubs with drought-deciduous or seasonally deciduous leaves must produce leaves, flowers, and fruits later in the year, a sequence which is disadvantageous should these processes not be completed when soil moisture is depleted during the warm season.

Further, shrubs which possess vasicentric tracheids or true tracheids are advantaged in drought years because water columns can be maintained by these tracheids, and branches and twigs can be maintained. Thus, dieback of branches may not occur, whereas it may in species without such tracheids in the same

region. Species with vascular tracheids have the potential advantage of maintaining branches in this way also, although foliage may be sacrificed. Large plant size cannot be achieved if frequent dry-season dieback occurs. Thereby the dominant shrubs of Mediterranean-type climates may be expected to be those in which vasicentric tracheids or true tracheids occur.

As noted earlier (Carlquist 1980), an appreciable number of species in the chaparral and desert regions of California have true tracheids (for a complete listing, see the terminal part of the discussion of the southern California flora, below). However, the species in the 1980 list do not include the majority of the characteristic shrubs of the chaparral and desert regions. Evidently only a few phylads with true tracheids have been able to make the transition from the wet areas where they likely originated (Carlquist 1975) to drier areas. For these few phylads, transition to a dry area must involve diminution in leaf size and probably many other morphological and physiological changes. This is illustrated by some of the Rosaceae (e.g., *Adenostoma*). Succulent underground roots from which shoots of finite duration sprout provide another mechanism, found in *Eriodictyon* (Hydrophyllaceae). Evidently the changes required are so sufficiently numerous and difficult that the few phylads bearing true tracheids have not been able to fill the available niches in areas with Mediterranean-type climates, even though they have filled some of them. One must remember that only a moderate proportion of dicotyledonous genera and families possess true tracheids (for a listing, see Carlquist 1984a).

Thus the bulk of Mediterranean-type climatic areas have been filled by phylads in which fiber-tracheids or libriform fibers (mostly the latter) are present as the imperforate tracheary element type. Such woods bulk large in the world flora. However, adaptation to habitats such as chaparral or desert—especially by evergreen shrubs—seems to have been accompanied by evolution of vasicentric tracheids in many of these groups. The native woody flora of southern California and the floras of other regions with Mediterranean-type climates almost seem like a selection of groups in which vasicentric tracheids occur. The listings below exemplify this. Mediterranean-type climates feature relatively little frost, so evergreen phylads are favored provided that drought-tolerance, such as that provided by vasicentric tracheids, can be achieved. Not all groups have this ability equally. Some groups seem to possess vasicentric tracheids universally (e.g., Sapotaceae), some seem to evolve them easily in species of dry areas although not all of a family has vasicentric tracheids (e.g., Rhamnaceae), whereas in some, vasicentric tracheids are not evolved easily or are related to production of vascular tracheids in great abundance (Asteraceae, Fabaceae). Some families in which vasicentric tracheids are very common or possibly universal do not tend to occur in areas with Mediterranean-type climates: Dipterocarpaceae and Sapotaceae, for example. However, presence of vasicentric tracheids in these families may permit them to survive drought in seasonally dry localities, such as the monsoon forests of southeast Asia where Dipterocarpaceae occur or the Hawaiian lowlands where Sapotaceae occur. Not all genera with vasicentric tracheids are evergreen: *Ribes* is a notable exception, but exceptions are few. In *Prunus*, the evergreen species have vasicentric tracheids, whereas the seasonally deciduous species (so far as known at present) lack them.

Some woody species in the chaparral have numerous narrow vessels in secondary xylem; some of these vessels have small perforation plates. These species

offer a condition not dissimilar to presence of vasicentric tracheids in potential safety. Thus, alternatives to vasicentric tracheids, true tracheids, or vascular tracheids can be said to exist, even though safety of the conductive system is not quite as great as it is in the species with tracheids of one kind or another.

The systematic occurrence of such features as narrow vessels, succulence, etc., in the southern California flora will be discussed in another paper. However, note should be taken that vasicentric tracheids and true tracheids are only two of many mechanisms for survival of dry seasons by woody species. Because this paper originated as part of a survey of the southern California flora, an attempt has been made to cover that flora carefully at the generic level and to investigate several species per genus where that seemed desirable. The abundance of vasicentric tracheids in the woody flora of southern California flora has, however, induced me to undertake a similar but preliminary survey of floras of other Mediterranean-type climatic areas for occurrence of vasicentric tracheids and true tracheids.

There is evidence, in these surveys, of increase in vasicentric tracheid presence with progressive dryness. For example, in Pittosporaceae only a minority of the species apparently have vasicentric tracheids. Those with only a few vasicentric tracheids occur in places of moderate dryness, such as the lowlands of Hawaii or New Caledonia. Species with more numerous vasicentric tracheids occur in areas with more marked aridity: *Pittosporum divaricatum* Cockayne from alpine New Zealand, or *P. phillyreoides* DC. There also appears to be increased abundance of vasicentric tracheids in vines as compared to shrubs, judging from *Clematis* (Fig. 11), in which libriform fibers are scarce, or from three scandent genera of Pittosporaceae: *Billardiera*, *Marianthus*, and *Sollya*.

The large number of genera and species discovered in this brief survey to have vasicentric tracheids leads to the conclusion that detailed search will reveal others. The pattern formed by new reports should prove a guide to where further records are most likely to be discovered. The discovery of vasicentric tracheids in so many families and genera in which they have not hitherto been recorded, including some large families (e.g., Ericaceae, Malvaceae, Rosaceae) and familiar genera (*Hedera*) suggests a need for a review of vasicentric tracheid occurrence in terms of the world flora. Such a review is offered in the terminal portion of this paper.

The occurrence of vasicentric tracheids has been overlooked in part because the wood anatomy of shrubs has been investigated less than that of trees. Vasicentric tracheids have been overlooked also, very likely, because these cells, when less frequent, are difficult to identify. Where vasicentric tracheids are abundant and different from the fibers they accompany—as in *Quercus* for example—there is no problem. Where vasicentric tracheids are relatively sparse and occur in the proportion of one file per vessel or where they are very similar in appearance to fiber-tracheids (in woods which have fiber-tracheids), vasicentric tracheids are easily overlooked. I have therefore included a guide to establishing presence of vasicentric tracheids in a section following the Materials and Methods section of this paper.

#### MATERIALS AND METHODS

Some of the wood sections and macerations necessary for the preparation of this survey were already on hand in the wood slide collection of the Rancho Santa

Ana Botanic Garden. Other wood samples were sectioned and macerated, however. Some of these were available dried, some available preserved in a 50% ethyl alcohol solution. Most woods could be sectioned rapidly and conveniently on a sliding microtome without any special treatment other than boiling in water in the case of the dried samples. Some woods which were especially hard (e.g., *Olneya tesota* Gray) required soaking in ethylene diamine, following the method of Kuchachka (1977). Other woods proved excessively soft (e.g., *Petrophytum caespitosum* [Nutt.] Rydb.), so a paraffin-embedding method involving softening (Carlquist 1982a) was invoked. Macerations are necessary to the identification of vasicentric tracheids, at least in some cases; these were prepared with Jeffrey's Fluid and stained with safranin. Sections were stained with safranin, but in most instances a counterstain was added; either haematoxylin or fast green proved an effective counterstain. These counterstains differentiate primary walls and thereby render pit membranes easily visible; thus, bordered pits, essential to the identification of vasicentric tracheids, can be seen. In addition to the survey of the southern California flora the woods selected represent shrubs in cultivation. The majority of these are species characteristic of Mediterranean-type climates. Some are evergreen shrubs which tend to be drought resistant in cultivation, which were suspected of having vasicentric tracheids (e.g., *Osmanthus fragrans* [Thunb.] Lour.). Some woods were collected from cultivated specimens in the Rancho Santa Ana Botanic Garden; these are designated by propagation numbers (which in turn are vouchered by herbarium specimens at RSA). Other woods of native species were collected in the wild near Claremont. Woods of many cultivated species were collected in Claremont; where these were well-known species, vouchers were not prepared. Some species utilized in this paper represent wood samples collected at a garden once owned by UCLA, but now abandoned, the Vavra Estate; these wood samples are not vouchered; identifications were made by Dr. Mildred E. Mathias. Some wood samples were collected at the Los Angeles State and County Arboretum, Arcadia, and are designated by the letters LASCA. The wood samples collected in cultivation were preserved in 50% ethyl alcohol; this has the advantage of revealing starch contents in parenchyma cells and in living fibers.

Herbarium specimens from the POM and RSA collections were utilized as sources for wood samples in some cases, where the specimen had sufficient wood and where access to the native area of a given species would have required excessive time or effort. Some dried wood samples derive from my wood sample collections made during travels in Australia, Chile, Hawaii, South Africa, and South America. Voucher specimens documenting these dried samples are cited in the review which terminates this paper.

Although cultivation may alter quantitative characteristics in wood of a given species, it does not appear to alter presence or absence of vasicentric tracheids.

#### IDENTIFICATION OF VASICENTRIC TRACHEIDS

When viewing a transection of a wood in which libriform fibers or fiber-tracheids are present, one may see that wide vessels are intermixed with narrower tracheary elements; the latter could be either vasicentric tracheids or narrower vessel elements, or both. If one suspects that they may be vasicentric tracheids and if the species has no growth rings, one may refer to a maceration to see if imperforate tracheary elements densely bearing bordered pits are, in fact, present in addition

to libriform fibers or fiber-tracheids. Observation of longitudinal sections (tangential sections are preferable) could then confirm presence of vasicentric tracheids.

A ring-porous wood in which fibers or fiber-tracheids are present may have wider vessels mixed with narrower tracheary elements, which may be narrow vessels or vasicentric tracheids. Such a wood might have imperforate cells densely bearing bordered pits (tracheids) only at the end of a growth ring. This can be established by viewing longitudinal sections (tangential sections are preferable to radial sections because one is more likely to see perforation plates in narrow tracheary elements, albeit in sectional view, in tangential sections). If tracheids are present only in latewood, vascular tracheids can be said to be present. An alternate procedure is that used by Yaghmaie and Catling (1984), that of macerating earlywood and latewood separately and examining for tracheids; where growth rings are narrow, this is not feasible. If vessels are intermixed with tracheids not only in latewood but also in earlywood of a ring-porous species bearing libriform fibers or fiber-tracheids, vasicentric tracheids rather than vascular tracheids may be said to be present (Fig. 6-10, 12, 14-16, 18-20). To be sure, one cannot easily see perforation plates at both ends of narrow vessel elements in a tangential section, and one could misidentify these as vasicentric tracheids if one failed to find a perforation plate at both ends of such cells. While one may be unable to see perforation plates in some few cells which are probably narrow vessel elements, observation of numerous cells bearing bordered pits but lacking perforation plates in a tangential section of a wood in which fiber-tracheids or libriform fibers are present should confirm presence of vasicentric tracheids. Also, one should be able to see, in macerations, some imperfectly separated groups of cells in which tracheids can be seen adjacent to vessel elements (one must be aware of the possibility of seeing a vascular tracheid adjacent to an earlywood vessel, however).

For example, in the wood of *Arctostaphylos auriculata* Eastw., examination of longisections shows that libriform fibers are present (Fig. 2, left of multiseriate ray; top right, to right of biseriate ray), although imperforate cells bearing bordered pits (and therefore tracheids) are also abundant. In the case of *Arctostaphylos*, bordered pits can easily be seen because pit cavities are often filled with dark-staining compounds (Fig. 2, 3, 4). If one views a transection (Fig. 1), most of the vessels appear to be solitary. Because *Arctostaphylos auriculata* occurs in a dry climate and has libriform fibers, one would expect that its vessels should be grouped unless vasicentric tracheids are present (Carlquist 1984a). In *A. auriculata*, one can see narrow cells with bordered pits in latewood (Fig. 4). These could be termed vascular tracheids (as was done in an earlier paper: Carlquist 1984a). However, narrow cells with bordered pits, cells which prove to be imperforate (when viewed in a tangential section), may be seen in earlywood as well (Fig. 3; note bordered pits in a series of cells between the vessel, top, and the vessel just below center). Thus, vasicentric tracheids must be said to be present in this wood. Another criterion in this species neglected in my 1984a paper is that imperforate cells (tracheids) do not form layers of narrow cells, exclusive of vessels, in the latewood. Rather, the tracheids occur intermixed with narrow vessels (Fig. 4).

The above account will enable the reader to see that presence of tracheids throughout a growth ring is the criterion used here for distinguishing vasicentric



tracheids from vascular tracheids. With a little practice, this distinction can easily be made.

Obviously a difficulty does arise in a wood in which vascular tracheids are clearly present in latewood, but in which they are so abundant that tracheids are present earlier in the growth ring as well as in the terminal portion; in such a wood, however, tracheids may not be present in the earliest portion of a growth ring. This could be regarded as basically an instance of vascular tracheid occurrence in which abundance of vascular tracheids overrides the usual definition and at least a few vasicentric tracheids must be said to be present. This condition obtains, for example, in most of the Asteraceae reported as having vasicentric tracheids in the southern Californian flora. The distinction between vasicentric and vascular tracheids is not merely an academic one in these cases. The *Haplopappus* species said to have vasicentric tracheids are evergreen species, even in dry chaparral or desert situations, whereas drought-deciduous Asteraceae from southern California typically lack vasicentric tracheids. The evolutionary introduction of tracheids into the mid-portion of a growth ring in a species which begins with vascular tracheids may be related to a shift from the drought-deciduous to the evergreen habit.

Introduction of what may have begun as vascular tracheids phylogenetically into progressively earlier portions of a growth ring may result ultimately in the pervasive presence shown by *Loricaria thuyoides* (Lam.) Sch. Bip., in which tracheids are so abundant that all tracheary elements are vessel elements or tracheids, and no libriform fibers, basic in the family to which *Loricaria* belongs, Asteraceae, are present (Carlquist 1961). In *Tetramolopium humile* Hillebr., also of Asteraceae, the process has not gone quite so far, and a few libriform fibers are present (Carlquist 1960). In most globular cacti—*Cochemia poselgeri* (Hildm.) Britt. & Rose and *Echinopsis multiplex* (Pfeiff.) Zucc. are notable by being exceptions—tracheids and narrow vessels but few or no libriform fibers are present (Gibson 1973). Although *Loricaria*, *Tetramolopium*, and the globular cacti have previously been cited as having vascular tracheids, they must now be redefined as having vasicentric tracheids in accordance with the above criteria. In all of these examples, growth rings are lacking and the plants are evergreen (although leafless in the case of the globular cacti).

Where a species has fiber-tracheids not very different from true tracheids, vasicentric tracheids are not easy to notice or to define. *Goupia glabra* Aubl. is said by Metcalfe and Chalk (1950) to have vasicentric tracheids, although *G. glabra* has fiber-tracheids which are very tracheidlike. However, vasicentric tracheids can be said to be present because around the vessels may be found tracheids which are more densely pitted than are the fiber-tracheids farther away from the vessels. This is also true in *Larrea* (Zygophyllaceae), *Protea* (Proteaceae), and *Verticordia* (Myrtaceae). In *Fagonia* (Zygophyllaceae), tracheids around the vessels are densely pitted, but so are the cells which form the background of the wood. Thus, although Metcalfe and Chalk claim vasicentric tracheids for all Zygophyllaceae, the distinction may have vanished in the case of *Fagonia*.

In some species with vasicentric tracheids, libriform fibers are rather scarce, as in the instances of *Clematis* and *Tetramolopium* mentioned above. If libriform fibers are lost altogether, as in *Loricaria*, the wood may appear to have true tracheids as the imperforate tracheary element type, but vasicentric tracheids must

be said to be present because the species is phylogenetically derived from an ancestry in which vasicentric tracheids became progressively more abundant. *Spiraea douglasii* Hook. (Rosaceae) has vasicentric tracheids and relatively small quantities of libriform fibers. *Petrophytum caespitosum* is a segregate of *Spiraea* which lacks libriform fibers. Are the tracheids in the wood of *Petrophytum* true tracheids (as they presumably are in other Rosaceae such as *Adenostoma* or *Heteromeles*), or are they vasicentric ones? This latter phyletic possibility, which has been realized in the case of *Loricaria* and most globular cacti, may have been realized in other instances as well although it is, I suspect, very rare in dicotyledons at large.

#### GEOGRAPHY OF VASICENTRIC TRACHEIDS AND TRUE TRACHEIDS

##### *Southern California*

When one views an area of typical chaparral, one sees an assemblage of species most of which have vasicentric tracheids. The pervasiveness of this phenomenon can be realized at such a locality as San Marcos Pass (Santa Barbara Co.), where the following conspicuous shrubby genera grow together: *Adenostoma*, *Arctostaphylos*, *Ceanothus*, *Dendromecon*, *Heteromeles*, *Malacothamnus*, *Prunus*, *Quercus*, *Rhamnus*, *Rhus*, *Ribes*, and *Salvia*. Of these, *Adenostoma* and *Heteromeles* have true tracheids, but all of the remainder of this assemblage have vasicentric tracheids. All of these genera are evergreen except for *Ribes*.

Southern Californian species in the following genera have vasicentric tracheids. The number of native southern Californian species studied is given in parentheses following the genus name. The collections which document these are listed in the review at the end of this paper. Indication (by means of asterisks) as to which genera and families are reported to have vasicentric tracheids for the first time in this paper will also be found in that review.

Acanthaceae: *Beloperone* (1).

Anacardiaceae: *Rhus* (3).

Asclepiadaceae: *Asclepias* (2).

Asteraceae: *Gutierrezia* (2); *Haplopappus* (4); *Lepidospartum* (1); other southern Californian species of the family may prove to have a few vasicentric tracheids, but vascular tracheids are characteristics of most dryland Asteraceae.

Berberidaceae: *Berberis* (2: see Fig. 9); probably all of the *Berberis* species formerly known under *Mahonia* possess vasicentric tracheids, since the mesic northern Californian species *B. nervosa* Pursh has abundant vasicentric tracheids.

Buddlejaceae: *Buddleja* (1).

Cactaceae: Gibson (1973) lists "vascular tracheids" (here interpreted as vasicentric tracheids) for one southern Californian species in each of the following genera: *Echinocactus*, *Echinocereus*, *Ferocactus*, and *Mammillaria*.

Chenopodiaceae: *Ceratoides* (= *Eurotia*) (1); *Grayia* (1: see Fig. 7). Vascular tracheids are abundant in these two genera, but vasicentric tracheids must be said to be present because some tracheids are intermixed with vessels; wood of two *Atriplex* species revealed no vasicentric tracheids.

Ericaceae: *Arbutus* (1); *Arctostaphylos* (Fig. 1-4); the 9 *Arctostaphylos* species studied are part of a synoptical collection of wood slides of the genus furnished

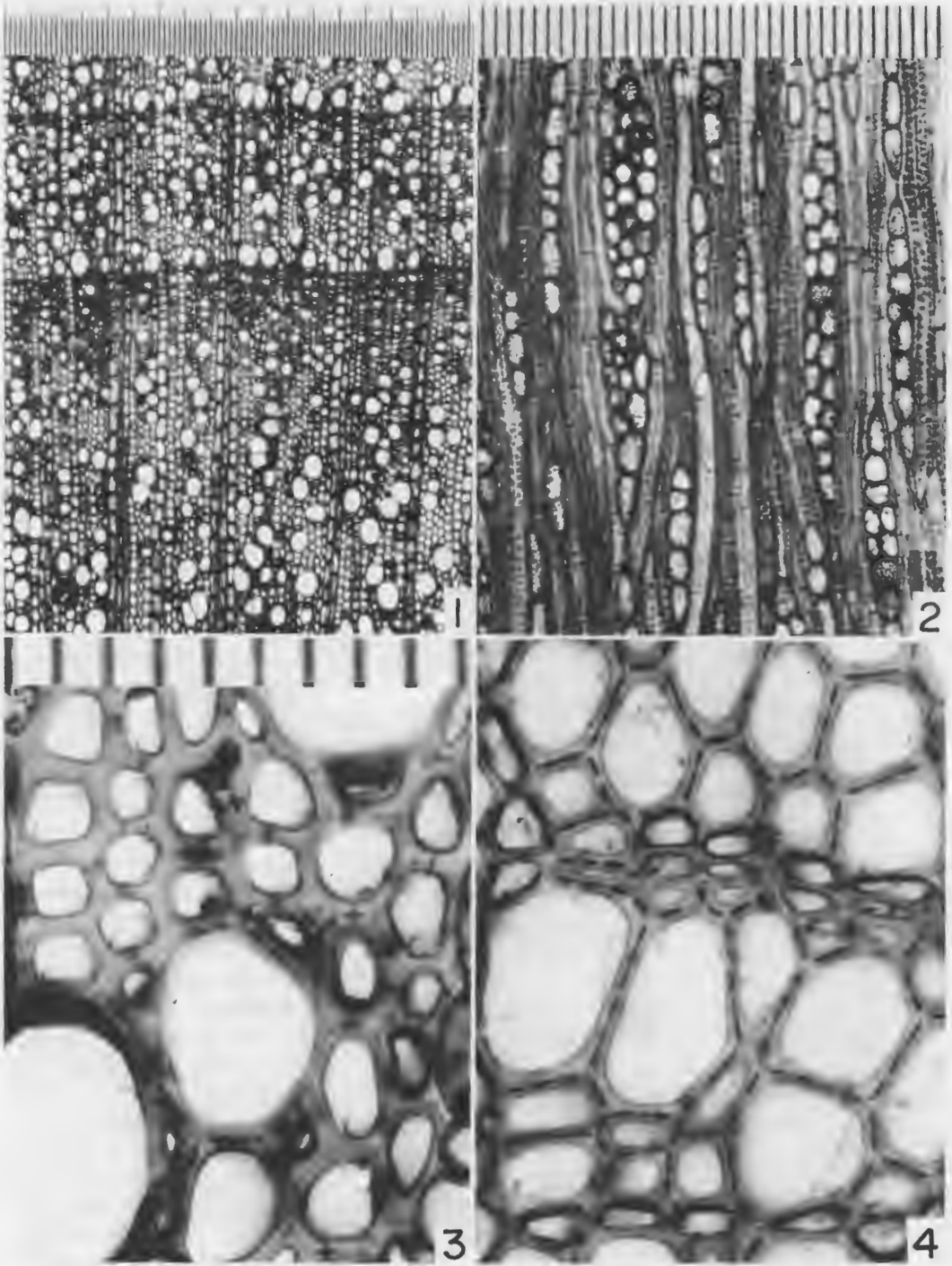


Fig. 1-4. Wood sections of *Arctostaphylos auriculata* (RSABG 11775).—1. Transection, showing growth rings; vessels are mostly solitary.—2. Tangential section. Most elongate cells in the section are vasicentric tracheids, but there is a vessel, center, and septate libriform fibers near top, to right and

by Dr. Gary Wallace; all species possess vasicentric tracheids; *Comarostaphylis* (1); *Ornithostaphylos* (1); *Xylococcus* (1).

Fabaceae: *Cassia* (1); in *Pickeringia* (1) vascular tracheids are abundant but a few vasicentric tracheids may be found; vasicentric tracheids were not found in the other southern Californian genera of Fabaceae.

Fagaceae: *Chrysolepis* (1); *Lithocarpus* (1); *Quercus* (1); vasicentric tracheids probably occur throughout these genera, judging from the statements of Metcalfe and Chalk (1950).

Frankeniaceae: *Frankenia* (2).

Grossulariaceae: *Ribes* (3); apparently vasicentric tracheids occur throughout the genus (Stern et al. 1970).

Lamiaceae: *Lepechinia* (1: see Fig. 8); *Monardella* (1); *Salazaria* (1); *Salvia* (3); *Trichostema* (3); vascular tracheids are more abundant than vasicentric tracheids in Lamiaceae; vasicentric tracheids, although not abundant, are more common than in Asteraceae.

Malvaceae: *Malacothamnus* (1); *Sphaeralcea* (1).

Papaveraceae: *Dendromecon* (1: see Fig. 10); *Romneya* (1).

Ranunculaceae: *Clematis* (1); as shown in Figs. 11 and 12, both narrow vessels and vasicentric tracheids are abundant.

Rhamnaceae: *Adolphia* (1); *Ceanothus* (Fig. 13, 14)—although only four species of *Ceanothus* were examined, these represent both subgenera and a wide range of ecology; *Colubrina* (1); *Condalia* (1); *Rhamnus* (2); *Zizyphus* (1).

Rosaceae: *Holodiscus* (2); *Prunus* (2); *Prunus fremontii*, which is seasonally deciduous, lacks vasicentric tracheids.

Rutaceae: *Cneoridium* (1: see Fig. 5, 6); *Thamnosma* (1).

Simaroubaceae: *Castela* (1).

Solanaceae: *Lycium* (3).

Ulmaceae: *Celtis* (1).

Verbenaceae: *Lippia* (1).

Zygophyllaceae: *Fagonia* (1); *Larrea* (1).

If the area of study were extended to include northern California, the following families and genera which have vasicentric tracheids could be added: Calycanthaceae (*Calycanthus*—vascular tracheids were claimed by Carlquist (1983), but because tracheids may be found earlier in growth rings as well, vasicentric tracheids must be said to be present); Rosaceae (*Spiraea*); Rutaceae (*Ptelea*); and Thymelaeaceae (*Dirca*).

True tracheids can be reported in the southern Californian woody flora for the following families and genera. Documentation is in the form of wood slides in the Rancho Santa Ana Botanic Garden wood-slide collection, as well as in the papers cited (see also Carlquist 1980).

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left of center.—3. Portion of earlywood from transection; most of the narrower cells are libriform fibers, but dark deposits in pit cavities reveal a series of vasicentric tracheids interconnecting the vessel, top, with the vessel below center.—4. Portion of latewood from transection; except for parenchyma cells, all cells (as shown by bordered pits) are vessels or vasicentric tracheids. (Magnification scale for Fig. 1 above Fig. 1 [finest divisions = 10  $\mu$ m]. Scale for Fig. 2 above Fig. 2 [divisions = 10  $\mu$ m]. Scale for Fig. 3, 4, above Fig. 3 [divisions = 10  $\mu$ m].)

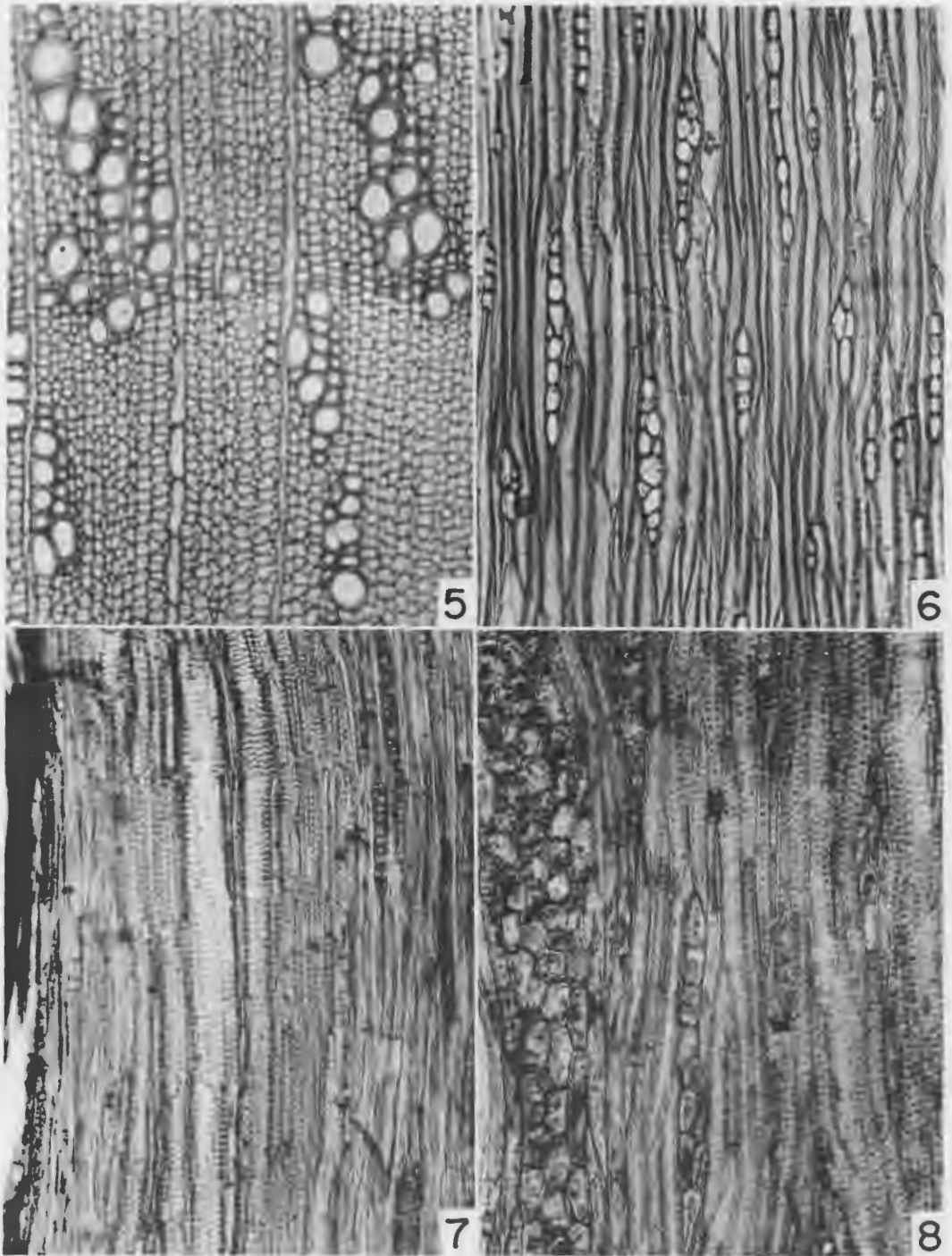


Fig. 5-8. Wood sections of Californian plants, showing vasicentric tracheid presence.—5-6. *Cneoridium dumosum* (RSABG 10059).—5. Transection, margin of growth ring near center; vasicentric tracheids are scattered among the vessels.—6. Tangential section; narrow vessels, vasicentric tracheids, and libriform fibers are present in about equal numbers.—7. *Grayia spinosa* (Thorne 44623, RSA),

Caprifoliaceae: *Lonicera*, *Symphoricarpos*.

Celastraceae: *Euonymus*, *Mortonia*.

Cistaceae: *Helianthemum*.

Cornaceae: *Cornus*.

Crossosomataceae: *Crossosoma*, *Forsellesia* (DeBuhr 1978).

Eleagnaceae: *Shepherdia*.

Ericaceae: *Ledum*, *Phyllodoce*, *Rhododendron*, *Vaccinium*.

Euphorbiaceae: *Tetracoccus*.

Fouquieriaceae: *Fouquieria* (Henrickson 1968).

Garryaceae: *Garrya*.

Hydrophyllaceae: *Eriodictyon* (Carlquist et al. 1983), *Turricula* (Carlquist and Eckhart 1984).

Koeberliniaceae: *Koeberlinia* (Gibson 1979).

Krameriaceae: *Krameria*.

Loasaceae: tracheidlike fiber-tracheids occur in *Eucnide* and *Petalonyx* (Carlquist 1984b).

Myricaceae: *Myrica*.

Oleaceae: *Menodora*.

Platanaceae: *Platanus*.

Polemoniaceae: *Eriastrum*, *Leptodactylon*, and *Phlox* (Carlquist et al. 1984).

Rosaceae: *Adenostoma*, *Amelanchier*, *Chamaebatia*, *Chamaebatiaria*, *Coleogyne*, *Cowania*, *Fallugia*, *Heteromeles*, *Lyonothamnus*, *Physocarpus*, *Purshia*, *Rosa*, *Rubus*.

Rubiaceae: *Galium*.

Saxifragaceae: *Fendlerella*, *Jamesia*, *Philadelphus*.

Simmondsiaceae: *Simmondsia* (Carlquist 1982b).

If the area of study were extended to northern California, the following genera with true tracheids could be added: Aristolochiaceae (*Aristolochia*); Ericaceae (*Cassiope*, *Menziesia*), Rosaceae (*Osmaronia*), and Saxifragaceae (*Carpenteria*). If gymnosperms were included, *Ephedra* would be an excellent example of vessels in a background of true tracheids. The vesselless gymnosperms of California have great safety in conduction because of their all-tracheid conductive system, and though they are an obvious example, we must not forget that this xylem conformation has permitted them to enter seasonally dry localities by virtue of making additional special adaptations (e.g., microphylls).

### *The Matorral of Chile*

The Mediterranean-type region in central Chile is not as large or as rich in species as are similar zones on other continents. However, vasicentric tracheids

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tangential section. To the left and right of the vessels are tracheids which, by virtue of their intermixture with vessels, are probably best termed vasicentric tracheids.—8. *Lepechinia calycina* (RSABG 14372), tangential section of wood. Almost all of the cells other than ray cells are narrow vessels or tracheids. Although latewood is represented, intermixture of tracheids with vessels occurs earlier in the growth ring as well, so vasicentric tracheids may be said to occur. (Fig. 5–8, magnification scale above Fig. 2.)



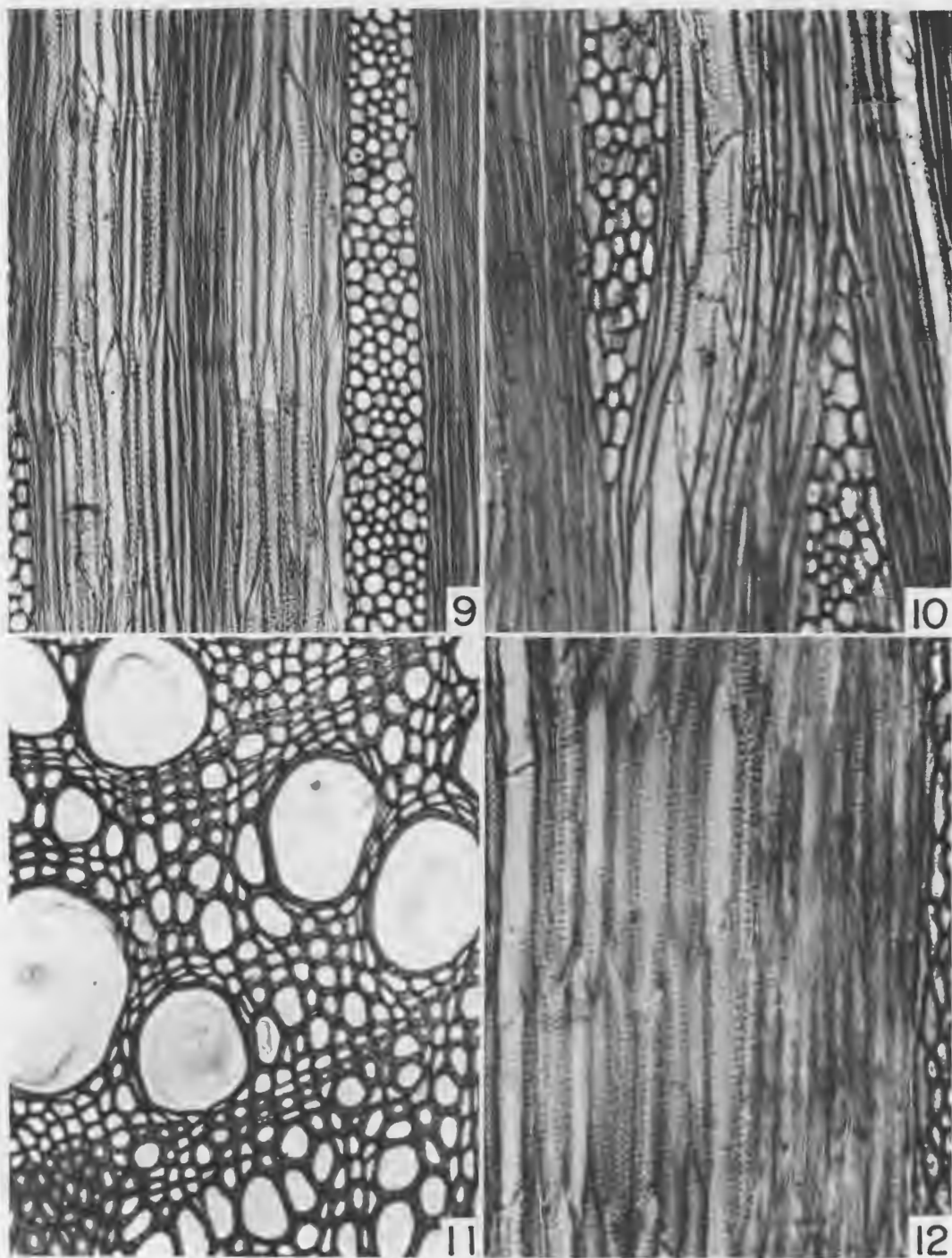


Fig. 9-11. Wood sections of Californian genera of Berberidales, showing vasicentric tracheid occurrence.—9. *Berberis nevinii* (RSABG 11910), tangential section; two bands of narrow vessels are shown; within these bands, vasicentric tracheids are about as numerous as the vessel elements.—10. *Dendromecon rigida* subsp. *rhamnoides* (Thorne 34845, RSA), tangential section. To the left of the

can be reported in the following families and genera (documentation in review section at end of paper).

Celastraceae: *Maytenus* (Fig. 15).

Flacourtiaceae: *Azara* (Fig. 16).

Frankeniaceae: *Frankenia*.

Grossulariaceae: *Ribes*.

Malesherbiaceae: *Malesherbia*.

Rhamnaceae: *Chacaya*, *Colletia*.

Santalaceae: *Myoschilos*.

Thymeleaceae: *Ovidia*.

Zygophyllaceae: *Larrea*.

Additional reports are likely to be found in the following families: Malvaceae (*Malacothamnus*); Rhamnaceae (several genera); and Solanaceae (vasicentric tracheids appear to be of universal occurrence in *Lycium*).

Genera in which true tracheids occur are listed below (documentation in the form of slides in the Rancho Santa Ana Botanic Garden wood-slide collection).

Desfontaineaceae: *Desfontainea*.

Escalloniaceae: *Escallonia*.

Krameriaceae: *Krameria*.

Monimiaceae: *Peumus*.

Rosaceae: *Kageneckia*, *Quillaja*.

Solanaceae: *Fabiana*.

### *Southwestern Australia*

The temperate portions of Australia contain remarkable examples of speciation in certain woody genera. Presence of vasicentric tracheids appears to be significant in the ability of these genera to succeed in this Mediterranean-type climate: many of the most conspicuous of woody Australian genera are in this list (documentation given in review section at end of paper). The fact that all of the genera below are evergreen is notable.

Casuarinaceae: *Casuarina*.

Fabaceae: *Hardenbergia*.

Frankeniaceae: *Frankenia*.

Lamiaceae: *Prostanthera*.

Loganiaceae: *Logania*.

Malvaceae: *Selenothamnus*.

Myrtaceae: *Baeckia* (at least in part), *Callistemon*, *Eucalyptus* (at least in part), *Eremaea*, *Leptospermum* (at least in part), *Melaleuca*, *Verticordia*.

Pittosporaceae: *Billardiera*, *Bursaria*, *Marianthus*, *Pittosporum*, *Sollya*.

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vessel, center, a slender vasicentric tracheid can be seen.—10, 11. *Clematis ligusticifolia* (RSABG 11765).—10. Transection. Large vessels, narrow vessels, and vasicentric tracheids are shown; the only libriform fibers are at lower left.—12. Tangential section; libriform fibers and ray portion at right; left half of photograph depicts a few vessels and numerous vasicentric tracheids. (Fig. 9–12, magnification scale above Fig. 2.)



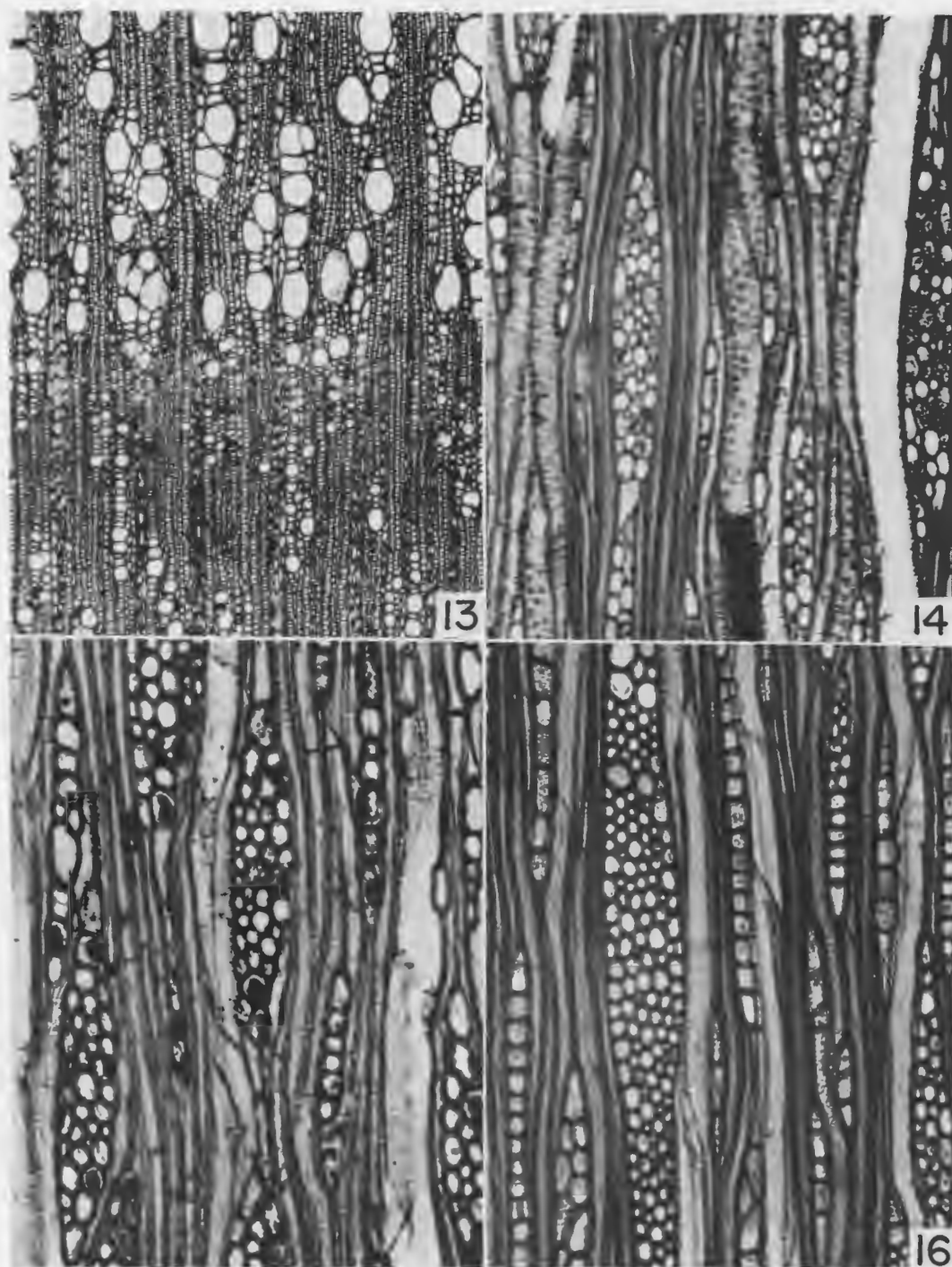


Fig. 13–16. Sections of Californian and Chilean woods with vasicentric tracheids.—13, 14. *Ceanothus thyrsiflorus* (RSAw-945).—13. Transection, earlywood above center; narrow vessels and vascular tracheids in limited number among the cells which are perceptible vessels.—14. Tangential section. Between the vessel, center, and the vessel at right are several vasicentric tracheids.—15.

Proteaceae: *Banksia*, *Dryandra*, *Grevillea* (Fig. 17, 18), *Hakea*, *Persoonia*, *Xylomelum*.

Rutaceae: *Boronia*, *Correa*, *Eriostemon*.

Santalaceae: *Santalum*.

Stylobasiaceae: *Stylobasium*.

Thymeleaceae: *Pimelea* (in part).

Tremandraceae: *Platytheca* (in part).

Violaceae: *Hybanthus*.

Vasicentric tracheids are to be expected in other genera of Myrtaceae and Proteaceae. In these two families, presence of vasicentric tracheids is not easy to detect because the fiber-tracheids which form the background of the fascicular xylem are not markedly less pitted than the vasicentric tracheids, where present; one must look for a difference in density of pits. Other temperate Australian groups in which vasicentric tracheids might be sought (because they are common in those groups elsewhere) include *Lycium* (Solanaceae) and various genera of Rhamnaceae and Rutaceae.

True tracheids characterize temperate shrubby Australian representatives of the following genera (documentation in the Rancho Santa Ana Botanic Garden wood-slide collection and also in Carlquist [1984a]).

Boraginaceae: *Halgania*.

Byblidaceae: *Byblis*.

Cephalotaceae: *Cephalotus*.

Dilleniaceae: *Hibbertia*.

Epacridaceae: *Andersonia*, *Cosmelia*, *Dracophyllum*, *Leucopogon*, *Lysinema*, and *Sphenotoma*.

Goodeniaceae: *Cooperhooia*, *Dampiera*, and *Scaevola*.

Loranthaceae: *Nuytsia*.

Proteaceae: *Isopogon*, *Stirlingia*.

Stackhousiaceae: *Stackhousia*.

Sterculiaceae: *Guichenotia*, *Lasiopetalum*.

The situation in Myrtaceae and Proteaceae is in need of more detailed study. *Tetratheca retrorsa* J. Thompson (Tremandraceae: cited as "*T. sp.*" in Carlquist 1977) and the species of *Tetratheca* studied by Heimsch (1942) have tracheids but lack libriform fibers, found in other Tremandraceae. There is a possibility that the condition in *Tetratheca* represents a derivation from the condition in *Platytheca verticillata* (Hueg.) Baill., which has vasicentric tracheids.

### *The Woody Mediterranean Flora*

The Mediterranean region is less rich in shrub species than southwestern Australia, southern Africa, or the Californian region. Nevertheless, an appreciable number of genera and species possess vasicentric tracheids. The review of wood

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*Maytenus boaria* (USw-8457). Tangential section, showing two vasicentric tracheids running top to bottom, center.—16. *Azara microphylla* (cult. Vavra Estate). Several vasicentric tracheids are present about ¼ of the way from the right edge of the photograph. (Fig. 13–16, magnification scale above Fig. 2.)

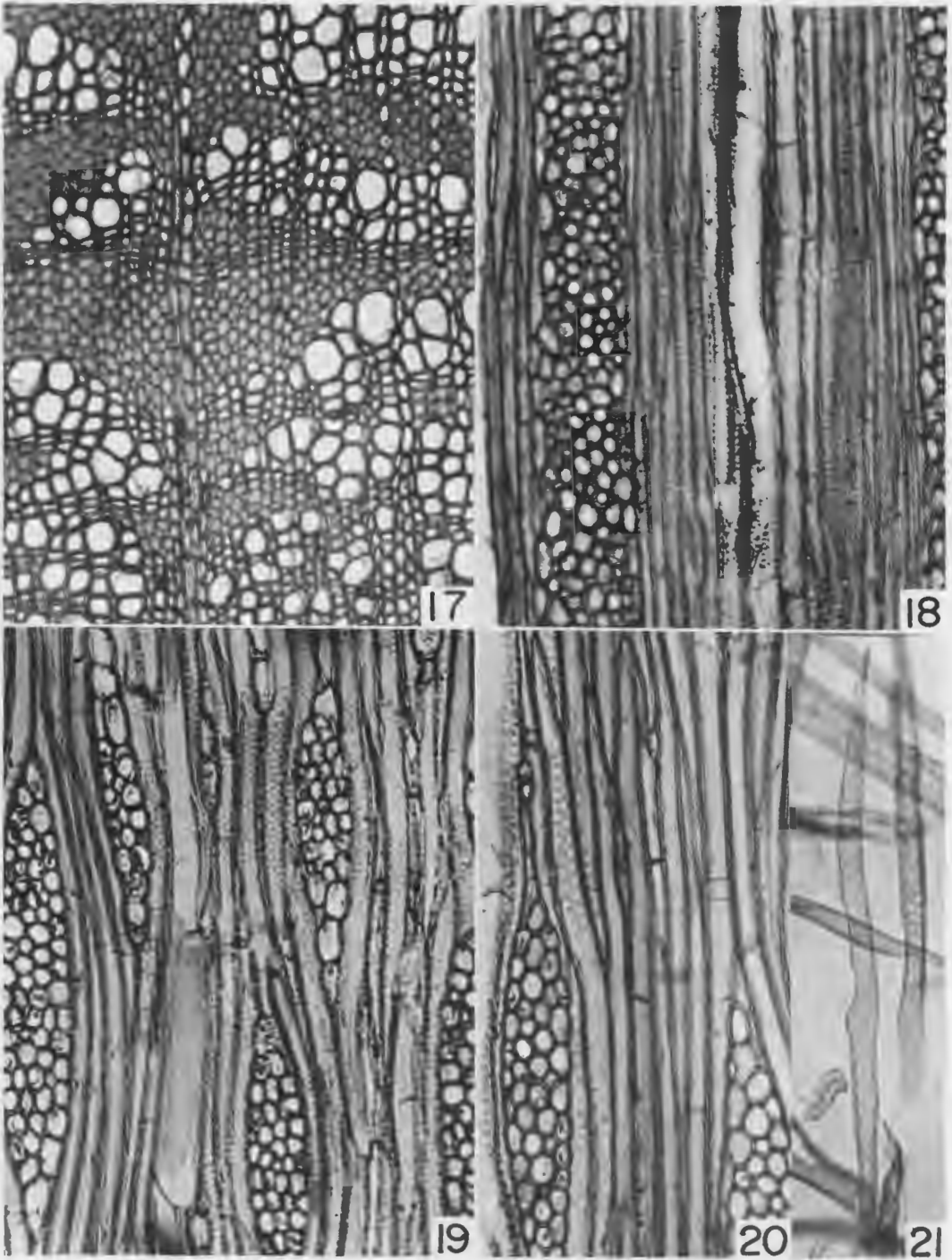


Fig. 17-21. Australian and European woods with vascentric tracheids.—Fig. 17, 18. *Grevillea obtusifolia* Meissn. (Carlquist 15851, RSA).—17. Transection. In the tangential bands of vessels are numerous vascular tracheids.—18. Tangential section. To the right and left of the vessels, center, are several layers of vascentric tracheids.—19. *Pittosporum phillyreoides* (Carlquist 5135, RSA), tangential

anatomy of European dicotyledons by Greguss (1959) is of some use in this regard. Greguss draws representative cells from the wood of the species he studied; these drawings are undoubtedly based on macerations. In a number of species, he figures both cells labeled as tracheids and cells labeled as libriform fibers. Woods with this condition could have either vasicentric tracheids or vascular tracheids (according to the definition I am using). Probably Greguss did not distinguish between these two conditions because the position of the tracheids within a growth ring (and most of these species are ring-porous) cannot be determined on the basis of a maceration alone. Therefore one can use Greguss's work as a starting point, even though he does not furnish information on mode of tracheid occurrence and one must therefore make new preparations and observations.

The following genera may be cited as having vasicentric tracheids in the Mediterranean region. Collections documenting the observations and literature citing vasicentric tracheids in species of this region are given in the terminal section of this paper.

Araliaceae: *Hedera* (Fig. 20, 21).

Asclepiadaceae: *Periploca*.

Balanitaceae: *Balanites*.

Cneoraceae: *Cneorum*.

Ericaceae: *Arbutus*, *Arctostaphylos*.

Fabaceae: *Spartium*.

Fagaceae: *Castanea*, *Quercus*.

Grossulariaceae: *Ribes*.

Hypericaceae: *Hypericum*.

Lamiaceae: *Lavandula*, *Rosmarinus*.

Oleaceae: *Ligustrum*, *Phillyrea*.

Rhamnaceae: *Rhamnus*.

Rosaceae: *Prunus*, *Spiraea*.

Santalaceae: *Osyris*.

Solanaceae: *Lycium*.

Thymeleaceae: *Daphne*, *Thymelea*.

Ulmaceae: *Ulmus* (and possibly also *Celtis*).

Genera in which true tracheids are present in the woody Mediterranean flora include:

Buxaceae: *Buxus*.

Celastraceae: *Euonymus*.

Cistaceae: *Cistus*, *Helianthemum*.

Dipsacaceae: *Pterocephalus*, *Scabiosa*.

Ericaceae: *Erica*.

Myrtaceae: *Myrtus*.

Rosaceae: *Amelanchier*, *Crataegus*, *Pyracantha*, *Rosa*, *Rubus*, *Sorbus*.

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section. Right  $\frac{3}{4}$  of photograph consists of narrow vessels intermixed with about an equal number of vasicentric tracheids.—20, 21. *Hedera helix* (cult. Claremont).—20. Tangential section. Three vasicentric tracheids are to the right of the multiseriate ray to the left of the photograph.—21. Portion of a maceration, showing two vasicentric tracheids (oriented vertically in the photograph). (Fig. 17–21, magnification scale above Fig. 2.)

### *Southern Africa*

In the area of southern Africa with a Mediterranean-type climate, numerous genera likely to possess vasicentric tracheids occur. I have been able to establish occurrence of vasicentric tracheids in species of the following genera from southern Africa (for documentation, see review at end of paper).

Apocynaceae: *Akocanthera*, *Carissa*.

Combretaceae: *Combretum*.

Pittosporaceae: *Pittosporum*.

Proteaceae: *Brabejum*, *Protea*.

Santalaceae: *Thesium*.

Stilbaceae: *Stilbe*.

Thymeleaceae: *Gnidia*.

Although original observations on vasicentric tracheid presence have not been made on the following genera native to southern Africa, vasicentric tracheids are known to occur in species of these genera from other regions: Asclepiadaceae (*Asclepias*); Balanitaceae (*Balanites*); Buddlejaceae (*Buddleja*, *Gomphostigma*); Clusiaceae (*Hypericum*); Connaraceae (various genera); Geraniaceae (various genera); Malvaceae (*Malvastrum*); Polygalaceae (*Securidaca*); Proteaceae (various genera); Rhamnaceae (*Rhamnus*, *Zizyphus*); Rutaceae (*Thamnosma* and probably other genera); Santalaceae (various genera); Sapotaceae (*Chrysophyllum*, *Mimusops*, *Sideroxylon*); Thymeleaceae (various genera).

The following genera from southern Africa are known to have true tracheids (wood slides documenting these located in the wood-slide collection of the Rancho Santa Ana Botanic Garden; see also citations for some of these families in Carlquist 1984a).

Bruniaceae: all genera.

Buxaceae: *Notobuxus*.

Cornaceae: *Cornus*.

Cunoniaceae: *Cunonia*, *Platylophus*.

Ericaceae: *Erica*, *Vaccinium*.

Geissolomataceae: *Geissoloma*.

Goodeniaceae: *Scaevola*.

Grubbiaceae: *Grubbia*.

Myrothamnaceae: *Myrothamnus*.

Myrtaceae: *Metrosideros*.

Oleaceae: *Menodora*.

Penaeaceae: *Brachysiphon*, *Endonema*, *Penaea*, *Sarcorolla*, *Sonderothamnus*.

Roridulaceae: *Roridula*.

Rosaceae: *Cliffortia*.

Genera from Rosaceae and Rubiaceae can doubtless be added to the above list. Especially noteworthy is the fact that the largest genus of temperate southern Africa, *Erica*, has true tracheids.

### *Other Temperate Regions*

As noted in the introductory section of this paper, vasicentric tracheids are not limited to regions with Mediterranean-type climates, even though this wood phenomenon certainly appears to be most common in those regions.

New Zealand has some dry scrublands and alpine regions, although moist forest bulks larger than it does in areas with Mediterranean-type climates. In New Zealand, vasicentric tracheids can be reported in the following genera: Araliaceae (*Pseudopanax*); Malvaceae (*Hoheria*); Oleaceae (*Nestegis*); Pittosporaceae (*Pittosporum*); Sapotaceae (*Planchonella*); and Violaceae (*Hymenanthera*). Some of these reports are new, others derive from Meylan and Butterfield (1978). From the figures of Meylan and Butterfield and from systematic considerations, one suspects vasicentric tracheids may be present in *Discaria toumatou* Raoul (Rhamnaceae) and *Mida salicifolia* A. Cunn. (Santalaceae). Genera with true tracheids are relatively common in the New Zealand flora. Most of these seem groups relictual in wet areas. This list includes: Chloranthaceae (*Ascarina*); Cunoniaceae (*Ackama*, *Weinmannia*); Epacridaceae (*Dracophyllum*); Griselinaceae (*Griselinia*); Icacinaceae (*Pennantia*); Monimiaceae (*Laurelia*); Myrtaceae (*Leptospermum*, *Metrosideros*, and *Neomyrtus*); Rubiaceae (*Coprosma*); Saxifragaceae (*Ixerba* and *Quintinia*); Scrophulariaceae (*Hebe*); and Winteraceae (*Pseudowintera*). This list seems relatively complete, thanks to the descriptions of Meylan and Butterfield (1978).

In Japan the climate is generally even moister than that of New Zealand, for scrublands in the ordinary sense are small in extent. The list of species in the Japanese flora known to possess vasicentric tracheids is, at present, a small one. It includes genera from the following families: Grossulariaceae (*Ribes*); Oleaceae (*Chionanthus*; *Osmanthus*); Pittosporaceae (*Pittosporum*); and Rosaceae (*Kerria*). Japan is notable for having a relatively large list of woody species in which true tracheids are present, and this seems to accord with the highly mesic climate (Carlquist 1975) and the relictual nature (unbroken history of occupancy of wet areas) likely for many of these species.

From China, one can add a few genera with vasicentric tracheids; these appear to characterize open areas more than wet forest, and include Apocynaceae (*Trachelospermum*); Araliaceae (*Tetrapanax*); Calycanthaceae (*Sinocalycanthus*, *Chimonanthus*); and Oleaceae (*Ligustrum*).

One is struck by the fact that many of the evergreen drought-resistant shrubs common in cultivation possess vasicentric tracheids (e.g., *Hedera helix* L., *Ligustrum lucidum* Ait., *Osmanthus fragrans* Lour., *Prunus caroliniana* Ait.) or true tracheids (*Calluna vulgaris* (L.) Hull, *Pyracantha coccinea* Roem.).

#### REVIEW OF VASICENTRIC TRACHEIDS

Metcalf and Chalk (1950, p. 1351) gave the first listing of families with vasicentric tracheids. They list 32 families, but three of these (Bonnetiaceae, Guttiferae, and Hypericaceae) are united by most authors now as Clusiaceae. Carlquist and Hoekman (1985) could not confirm presence of such tracheids in Staphyleaceae. Thus 29 families appear validly reported by them. In a later listing (Metcalf and Chalk 1983) only a single family, Geraniaceae, is added to this earlier list and Hypericaceae is removed (presumably because of merger with Guttiferae, called Clusiaceae here). The new listing I am offering below is based on the definition of vasicentric tracheid given in the introductory section of this paper. Each genus or family for which vasicentric tracheids are reported for the first time in the present paper is preceded by an asterisk (\*). Standard herbarium and xylarium abbreviations are used. Species cited without collector represent unvouchered collections I have made from the localities indicated.

- \***Acanthaceae:** \**Beloperone californica* Benth. (RSABG 13820) has vascular tracheids and a few vasicentric tracheids; \**Thunbergia alata* Bojer (LASCA 81-S-42) has a few vasicentric tracheids as well as numerous narrow vessel elements similar to the vasicentric tracheids.
- \***Anacardiaceae:** \**Rhus ovata* Wats. (San Marcos Pass, Calif.) has a few vasicentric tracheids as well as numerous narrow vessel elements similar to the vasicentric tracheids.
- \***Ancistrocladaceae:** \**Ancistrocladus tectorius* Merrill (Carlquist 4375, RSA) and *A. wallichii* Planch. (Colani 21218, UC) have vasicentric tracheids like those of Dipterocarpaceae.
- Apocynaceae:** \**Akocanthera venenata* Don (cult. Santa Barbara); \**Beaumontia grandiflora* Wall. (cult. Vavra Estate); \**Carissa arduina* Lam. (cult. Vavra Estate); \**Stephanotis grandiflora* Brogn. (cult. LASCA); \**Trachelospermum jasminoides* Lem. (cult. Claremont); earlier reports for the family include *Condylocarpon* and *Kopsia* (Janssonius 1906–1936).
- \***Araliaceae:** \**Hedera helix* (cult. Claremont); \**Pseudopanax lessonii* (DC.) Koch (cult. Santa Barbara); \**Tetrapanax papyrifera* Koch (cult. Berkeley).
- Asclepiadaceae:** \**Asclepias albicans* Wats. (Aw-4401); *A. erosa* Torr. (Bissing 219, RSA), and \**Tacazzea apiculata* Oliver (cult. LASCA); Metcalfe and Chalk (1950) report *Leptadenia* and *Periploca*.
- Asteraceae:** \**Argyroxiphium kauense* (Rock & Neal) Deg. & Deg. (Carlquist 2110, RSA); \**Dubautia menziesii* (Gray) Keck (Carlquist H17, UC); \**Gutierrezia microcephala* (CD.) Gray (Carlquist 630, RSA); \**Haplopappus acradenius* (Greene) Blake (Carlquist 931, RSA); *H. cooperi* (Gray) Hall (Armstrong 1032, RSA); *H. cuneatus* Gray (Tilforth 1720, RSA); *H. ericoides* (Less.) H. & A. (Balls 21446, RSA); \**Lepidospartum squamatum* (Gray) Gray (Carlquist 621, RSA); \**Loricaria thuyoides* (Yw-20753); \**Tetramolopium humile* (Carlquist H18, UC). Comments on *Loricaria* and *Tetramolopium* can be found in the section above on identification of vasicentric tracheids. I was unable to confirm the report by Metcalfe and Chalk (1950) of vasicentric tracheids in *Wedelia* or that by Metcalfe (1935) for *Brachylaena*; these reports may refer to what I am terming vascular tracheids.
- Balanitaceae:** vasicentric tracheids are reported for four species of *Balanites* by Parameswaran and Conrad (1982).
- \***Berberidaceae:** vasicentric tracheids are present abundantly in *Berberis haematocarpa* Woot. (David French wood coll., s.n.), *B. nervosa* (Bissing 262, RSA), and *B. nevinii* Gray (RSABG 11910), and \**Nandina domestica* Thunb. (cult. Claremont).
- \***Betulaceae:** Yaghmaie and Catling (1984) report vasicentric tracheids (as “vascular tracheids”) for *Alnus* spp., *Betula* spp., *Carpinus* spp., and *Corylus* spp. I am interpreting vasicentric tracheids as present because the authors have found tracheids in earlywood as well as in latewood.
- \***Bignoniaceae:** \**Doxantha unguis-cati* Rehd. (cult. U. Hawaii) has vasicentric tracheids in appreciable numbers; they are relatively rare in other Bignoniaceae.
- Boraginaceae:** vasicentric tracheids are claimed to be frequent in *Ehretia* by Metcalfe and Chalk (1950). Gottwald (1982) convincingly reports vasicentric tracheids in *Lepidocordia punctata* Ducke of the subfamily Ehretioidese.

\***Buddlejaceae:** \**Buddleja utahensis* Cov. (Wolf 9833, RSA). Mennega (1980) reports "tracheids" for the genera *Buddleja* and *Gomphostigma*; these are probably vasicentric tracheids.

\***Cactaceae:** as discussed above in connection with Californian cacti, where tracheids predominate as the conductive cell type in globular cacti to the exclusion of libriform fibers, and where these tracheids are scattered among vessels and not present at the end of growth rings, vasicentric tracheids must be said to be present. Such tracheids are reported (as "vascular tracheids" for 38 species of 16 genera by Gibson [1973]).

**Calycanthaceae:** vasicentric tracheids are reported for both *Calycanthus* and *Chimonanthus* by Metcalfe and Chalk (1950). As noted earlier, I concur.

**Capparaceae:** I have reported vasicentric tracheids for *Oceanopapaver* (Schmid et al. 1985). This is an instance in which vascular tracheids are abundant and occasional tracheids, which must be termed vasicentric tracheids, occur earlier in growth rings as well. Examination of various other Capparaceae has revealed no other instances of vasicentric tracheids (vascular tracheids occur in *Isomeris*).

**Casuarinaceae:** Moseley (1948) reports vasicentric tracheids throughout the genus (species not given for this feature); he finds different degrees of abundance of vasicentric tracheids in different species. El-Osta et al. (1981) report vasicentric tracheids for *Casuarina cunninghamiana* Miq. and *C. glauca* Sieb. in Spreng. I have observed them in *C. pinaster* C. A. Gardn. (Carlquist 5980, RSA).

**Celastraceae:** vasicentric tracheids can be reported for \**Maytenus boaria* Molina (USW-8457). The only previous report for the family is that of Janssonius (1906–1936) for *Microtropis bivalvis* Wall.

\***Chenopodiaceae:** *Ceratoides lanata* (Pursh) J. T. Howell (RSABG 14393) and *Grayia spinosa* (Hook.) Moq. (Thorne 44623, RSA) have vascular tracheids in latewood, but just before this vessels mixed with tracheids which I am terming vasicentric tracheids.

**Clusiaceae** (including **Bonnetiaceae** and **Hypericaceae**): Metcalfe and Chalk (1950) reported vasicentric tracheids in a group of genera which they term "Group B" (*Calophyllum*, *Kayea*, *Mammea*, *Mesua*, and *Poeciloneuron*) as well as in genera of **Hypericaceae** s.s. (*Harungana*, *Hypericum*, *Vismia*, and, less abundantly, *Cratoxylon*). Confirmations are offered by Baas (1970) and Gibson (1980). Metcalfe and Chalk (1950) noted vasicentric tracheid presence in *Bonnetia* under **Bonnetiaceae**.

\***Cneoraceae:** Heimsch (1942) reported that "vascular tracheids probably occur" in *Cneorum tricoccum* L.; material I have studied (cult. Orpet Park, Santa Barbara) has what I definitely would term vasicentric tracheids.

**Combretaceae:** vasicentric tracheids were reported for *Strephonema* by Metcalfe and Chalk (1950); Vliet (1979) confirms this report, and also reports what I would term vasicentric tracheids for *Calopyxis*, *Calycopteris*, *Combretum*, *Guiera*, and *Thiloa*.

**Connaraceae:** vasicentric tracheids were reported by Metcalfe and Chalk (1950) for *Byrsocarpus*, *Cnestidium*, *Connarus*, *Manotes*, and *Rourea*. Dickison (1972) confirms their presence in the family.

**Dipterocarpaceae:** vasicentric tracheids were reported by Metcalfe and Chalk



(1950) for *Balanocarpus*, *Dipterocarpus*, *Doona*, *Hopea*, *Parashorea*, *Pentacme*, and *Shorea*. There has been no thorough review of vasicentric tracheid occurrence in the family since.

\*Ericaceae: vasicentric tracheids may be reported in *\*Arbutus menziesii* Pursh (Bissing 224, RSA); *A. xalapensis* HBK. (USw-1905); clearly present in *A. andrachne* and *A. unedo* also, judging from the drawings of Greguss (1959); *\*Arctostaphylos* (present in all species of a synoptical collection of wood section and maceration slides of the genus presented to the Rancho Santa Ana Botanic Garden by Dr. Gary Wallace); *\*Comarostaphylis diversifolia* (Parry) Greene (Wallace 1387, RSA); *\*Ornithostaphylos oppositifolia* (Parry) J. K. Small (Wallace 1384, RSA); *\*Xylococcus bicolor* Nutt. (Wallace 1380, RSA). All of these belong to Arbutoideae.

\*Erythroxylaceae: vasicentric tracheids can be reported in *\*Erythroxylum monogynum* Roxb. (USw-5464).

\*Fabaceae: *\*Cassia armata* (Carlquist 15858, RSA) has vasicentric tracheids in addition to narrow vessels; *\*Hardenbergia violacea* (Schneev.) Stearn (cult. LASCA), *\*Spartium junceum* L. (San Antonio Canyon), and *\*Wisteria sinensis* Sweet (LASCA 68-P-29) have many narrow vessels plus some vasicentric tracheids. In *\*Pickeringia montana* Nutt. (Balls 2185, RSA) vascular tracheids are abundant in latewood, but a few tracheids adjacent to vessels earlier in growth rings must be termed vasicentric tracheids.

Fagaceae: vasicentric tracheids are characteristically present in all genera except *Fagus* and *Nothofagus* according to Metcalfe and Chalk (1950). I have observed them in the Californian species *Chrysopsis sempervirens* (Kell.) Hjelmq. (Mt. San Jacinto), *Lithocarpus densiflora* (H. & A.) Rehd. (RSABG 7532), and *Quercus dumosa* Nutt. (Claremont).

\*Flacourtiaceae: *Azara microphylla* Hook. f. (cult. Vavra Estate) has a few vasicentric tracheids throughout the wood.

\*Frankeniaceae: the alphabetical order of the following species is also the order of increasing abundance of vasicentric tracheids: *\*Frankenia grandifolia* C. & S. var. *campestris* Gray (Gilman 4000, POM); *F. grandifolia* var. *grandifolia* (Thorne 34937, RSA); *F. interioris* Ostf. (Carlquist 5793, RSA); *F. patagonica* Speg. (O'Donell 3324, RSA).

Geraniaceae: this family is listed by Metcalfe and Chalk (1983), but no genera or species are given. I can report vasicentric tracheids for *\*Geranium arboreum* Gray (Carlquist 2130, RSA), *G. cuneatum* Hillebr. (Carlquist 2098, RSA), and *G. tridens* Hillebr. (Carlquist 546, RSA).

Goupiaceae: reported for the family by Metcalfe and Chalk (1950); *Goupia glabra* (Stahel 73, RSAw) shows a single layer of vasicentric tracheids around vessels.

Grossulariaceae: vasicentric tracheids are claimed for the genus *Ribes* without exceptions by Stern et al. (1970). I observed them in *R. aureum* Pursh (RSABG 6539), *R. cereum* Dougl. (Everett 21900, RSA), and *R. montigenum* Mc. Clat. (Warnock 9, RSA).

\*Lamiaceae: collections found to have vasicentric tracheids include *\*Lavandula officinalis* Chaix & Vill. (Neugebauer 2, RSA); *\*Lepechinia calycina* (Benth.) Epling (RSABG 14372); *\*Monardella linoides* Gray subsp. *viminea* (Greene) Abrams (RSABG 6483); *\*Prostanthera* sp. (from Australia, Carlquist 5160,

RSA); *\*Rosmarinus officinalis* L. (cult. Claremont); *\*Salvia apiana* Jepson (Carlquist 15799, RSA); *S. dorri* (Kell.) Abrams (Carlquist 15860, RSA); *S. mellifera* Greene (Carlquist 15800, RSA); *\*Trichostema lanatum* Benth. (RSABG 13735). Vasicentric tracheids were absent in *Hyptis emoryi* Torr. (RSABG 10020). Where present in the family, vasicentric tracheids are less abundant than vascular tracheids, which also are present in the species which possess vasicentric tracheids.

Lauraceae: Janssonius (1906–1936) reported vasicentric tracheids in *Iteadaphne confusa* Bl., *Phoebe declinata* Nees, and *Litsea* spp.

Linaceae: vasicentric tracheids were reported by Metcalfe and Chalk (1950) for *Ctenolophon* and *Ixonanthes*.

\*Loganiaceae: *\*Logania albiflora* (Andr.) Druce (Thorne 20432, RSA); these are likely what Mennega (1980) reports as “tracheids” for this species, and by the same token we can add here as reports of vasicentric tracheids her mention of tracheids in *Strychnos* and *Usteria*.

\*Malesherbiaceae: vasicentric tracheids are present in *\*Malesherbia densiflora* Phil. (Ricardi 658, RSA); *M. fasciculata* Don (Simon 385, RSA); *M. lirana* C. Gay (Morison 17054, UC); and *M. tubulosa* (Cav.) McBr. (Goodspeed 33148, UC).

\*Malpighiaceae: limited numbers of vasicentric tracheids occur in *\*Stigmaphyllon ledifolium* (HBK.) Small (Aw-19423) and *S. puberum* (L. C. Rich.) A. Juss. (Aw-19422).

\*Malvaceae: vasicentric tracheids are present in *\*Hoheria lyallii* Hook. f. (Chapman 258505, RSA); *\*Malacothamnus fasciculatum* (Nutt.) Greene (Carlquist 15855, RSA); *\*Selenothamnus helmsii* (F. Muell. & Tate) Melville (Craven 5033, RSA); and *\*Sphaeralcea emoryi* Torr. (Ewan 4147, POM). Vasicentric tracheids are apparently absent in *Hoheria populnea* A. Cunn. (Bracelin 14587, RSA).

Myrtaceae: Metcalfe and Chalk (1950) reported vasicentric tracheids for “most of the genera, but not observed or clearly distinguished from the fiber-tracheids in some species of *Backhousia*, *Baeckia*, *Decaspermum*, *Eucalyptus*, *Gomidesia*, *Jambosa*, *Kroki*, *Myrceugenia*, *Myrtus*, *Syncarpia*, *Syzygium*, and *Xanthostemon*.” I can report vasicentric tracheids in *\*Callistemon speciosus* DC. (cult. Claremont); *\*Eremaea pauciflora* (Endl.) Druce (Carlquist 5944, RSA); *\*Leptospermum firmum* (Schau.) Benth. (Carlquist 5708, RSA); *\*Melaleuca* sp. (Carlquist 6007, RSA); *\*Psidium guajava* L. (cult. Vavra Estate); and *\*Verticordia chrysantha* Endl. (Lathrop 502, RSA). Further study of vasicentric tracheid occurrence in Myrtaceae would be of interest because these cells may play a very important role in the capability of *Eucalyptus* (and other genera) to withstand excessive drought, and to assume arboreal habits under these conditions.

Ochnaceae: small numbers of vasicentric tracheids are reported in *Lophira* by Metcalfe and Chalk (1950).

Olacaceae: vasicentric tracheids are reported for *Olax* by Metcalfe and Chalk (1950), but I could not confirm this in species from southwestern Australia.

Oleaceae: vasicentric tracheids are reported by Metcalfe and Chalk (1950) for *Chionanthus retusus* Lindl. and *Phillyrea media* L.; they also occur (reported as “vascular tracheids”) in *Nestegis cunninghamiana* Hook. f. and *N. lan-*

*ceolata* (Hook. f.) L. Johnson (Meylan and Butterfield 1978) and in *Ligustrum lucidum* (Parameswaran and Gomes 1981). In addition, I have observed them in *\*Osmanthus fragrans* (cult. Claremont) and *O. ilicifolia* Mouillef (cult. Vavra Estate).

**\*Papaveraceae:** vasicentric tracheids can be reported for two Californian genera:

*\*Dendromecon rigida* Benth. ssp. *ramnoides* (Greene) Thorne (Thorne 34845, RSA); and *\*Romneya coulteri* Harv. (Carlquist 15820, RSA).

**\*Passifloraceae:** Ayensu and Stern (1964) state that arboreal Passifloraceae have both libriform fibers and fiber-tracheids (the latter with conspicuous bordered pits and adjacent to vessels where neighboring cells mentioned). These data can, in my opinion, only be interpreted as evidence of vasicentric tracheid presence. Absence of libriform fibers in most of the scandent species of *Passiflora* would then be an example of derivation of a libriform-fiber-free condition (in which imperforate cells could probably be termed tracheids rather than fiber-tracheids), reminiscent of the accelerated loss of libriform fibers in *Clematis* (Ranunculaceae).

**\*Pittosporaceae:** I can report vasicentric tracheids in *\*Billardiera bicolor* (Putterlick) F. M. Bennett (Carlquist 5932, RSA); *\*Bursaria incana* Lindl. (FPaw-7151); *\*Marianthus procumbens* Benth. (Carlquist 5532, RSA); *Pittosporum bicolor* Hook. (FPaw-773); *P. divaricatum* (coll. Alan Marks, s.n., Arthur's Pass); *P. glabratum* Lindl. (FPaw-14731); *P. glabrum* H. & A. (FPaw-21961); *P. mouanum* Guill. (Carlquist 15603, RSA); *P. napaliense* Sherff (Stern & Carlquist 1344, RSA); *P. pancheri* Brogn. & Gris (Carlquist 5320, RSA); *P. phillyreoides* (Carlquist 5135, RSA); *P. ralphii* Kirk (WZw, s.n.); *P. tobira* (Thunb.) Ait. f. (cult. Claremont); *P. turneri* Petrie (WZw, s.n.); *P. undulatum* Vent. (cult. Claremont); *P. viridiflorum* Sims (Carlquist 4998, RSA); *\*Sollya heterophylla* (all collections listed in Carlquist 1981).

**Polygalaceae:** Metcalfe and Chalk (1950) report vasicentric tracheids in *Securidaca*; I can add *\*Monnina* sp. (cult. U.C. Berkeley Botanic Garden).

**Proteaceae:** Metcalfe and Chalk (1950) cite reports by Chalk et al. (1935), Kanehira (1921), and Welch (1925) for vasicentric tracheids in the genera *Darlingia*, *Faurea*, *Grevillea*, *Helicia*, *Musgravea*, and *Stenocarpus*. To this list may be added the following new reports: *\*Banksia grandis* Willd. (cult. Orpet Park, Santa Barbara); *\*Brabejum stellatifolium* L. (Carlquist 4970, RSA); *\*Dryandra runcinata* Meissn. (Carlquist 5981, RSA); *Grevillea obtusifolia* Meissn. (Carlquist 15851, RSA); *\*Hakea cristata* R. Br. (cult. Orpet Park, Santa Barbara); *H. suaveolens* R. Br. (cult. Claremont); *\*Persoonia longifolia* R. Br. (Carlquist 6058, RSA); *\*Protea* spp. (all species in a synoptical collection of wood slides of South African species of *Protea*, donated by Miss Joan van Reenen, have vasicentric tracheids); *\*Xylomelum occidentale* (Carlquist 5889, RSA). Vasicentric tracheids differ from fiber-tracheids only in slightly greater diameter and greater density of bordered pits. In this respect, the situation in Proteaceae is similar to that in Myrtaceae.

**Quiinaceae:** Metcalfe and Chalk (1950) reported vasicentric tracheids in *Quiina* and *Touroulia*. Gottwald and Parameswaran (1967) confirmed these and added *Lacunaria*.

**\*Ranunculaceae:** *\*Clematis ligusticifolia* Nutt. (RSABG 11765) has numerous vasicentric tracheids mixed with narrow vessels.

**Rhamnaceae:** not included in the listings of Metcalfe and Chalk (1950); the

only prior report of vasicentric tracheids in the family is that of Braun (1970) for *Rhamnus cathartica* L. Vasicentric tracheids are not uncommon in shrubby Rhamnaceae, however, and the following new reports can be made: \**Adolphia californica* Wats. (Balls 20389, RSA); \**Ceanothus arboreus* Greene (Carlquist & Thorne 1822, RSA); *C. leucodermis* Greene (Wolf 2140, RSA); *C. thyrsiflorus* Esch. (Balls 23547, RSA); \**Chacaya trinervis* (Gill) Escalante (Gibson 3040, RSA); \**Colletia cruciata* Hook. (cult. Vavra Estate); \**Colubrina californica* Jtn. (Jaeger Oct. 30, 1938, POM); \**Condalia globosa* Jtn. (Thorne 33606, RSA); *Rhamnus californica* Esch. (Bissing 264, RSA); *R. crocea* Nutt. (Claremont); \**Zizyphus parryi* Torr. (David French wood coll., s.n.); vasicentric tracheids are absent in *Z. jujuba* Mill. (USw-5847).

\*Rosaceae: vasicentric tracheids can be reported in \**Holodiscus discolor* (Pursh) Maxim. (David French wood coll., s.n.); *H. microphyllus* Rydb. (Carlquist 15847, RSA); \**Kerria japonica* DC. (inferred from drawings in Greguss 1959); \**Prunus caroliniana* (cult. Claremont); *P. ilicifolia* (Nutt.) Walp. (San Antonio Canyon); *P. laurocerasus* (cult. Claremont); *P. lyoni* (Eastw.) Sarg. (RSABG 10841); \**Spiraea douglasii* (RSABG 14790).

Rutaceae: Metcalfe and Chalk (1950) report vasicentric tracheids in *Acradenia*, *Choisya*, and *Skimmia*. To this list can be added the following new reports: \**Boronia alata* Sm. (Carlquist 5541, RSA); *B. denticulata* Sm. (Carlquist 5770, RSA); *B. oxyantha* Turcz. (Carlquist 5705, RSA); \**Cneoridium dumosum* (Nutt.) Hook. f. (RSABG 10059); \**Correa speciosa* Ait. (cult. Santa Barbara); \**Eriostemon spicatus* A. Rich. (Carlquist 5945, RSA); \**Ptelea crenulata* Greene (Bissing 230, RSA); \**Thamnosma montana* Torr. & Frem. (Hitchcock 6250, RSA).

Santalaceae: Metcalfe and Chalk (1950) report vasicentric tracheids in *Jodina* and *Myoschilos*, but add that "some cells suggesting vasicentric tracheids" occur in *Eucarya*, *Exocarpus*, *Osyris*, and *Santalum*. I can report vasicentric tracheids in a South African species of *Thesium* (Carlquist 4627a, RSA), in which they resemble fiber-tracheids closely.

\*Sapindaceae: limited numbers of vasicentric tracheids occur in *Serjania* aff. *glabrata* HBK. (cult. U. Hawaii).

Sapotaceae: Metcalfe and Chalk (1950) state that vasicentric tracheids are "commonly present, numerous in *Bumelia*, *Madhuca*, and *Pouteria*, and present, mixed with very small vessels and vascular tracheids, in several other genera." For citation of Kukachka's 38 papers on wood anatomy of neotropical Sapotaceae, the last in the series (Kukachka 1982) may be consulted. Kukachka's data show that vasicentric tracheids occur throughout the family but vary in abundance according to genus.

Simaroubaceae: vasicentric tracheids have been reported by Webber (1936) for *Alvaradoa*, *Castela*, and *Holacantha*. The *Castela* reported for the California flora above has been transferred from *Holacantha*.

\*Solanaceae: vasicentric tracheids are abundant in woods of the following species: *Grabowskya* sp. (PRFw-10560); \**Lycium brevipes* (RSABG 14429); *L. cestroides* Schlect. (PRFw-10582); *L. elongatum* Miers (PRFw-10520); *L. europeum* L. (PRFw-24676); *L. fremontii* Gray (RSABG 7801). Because these species are so uniform in abundance of vasicentric tracheids, presence of vasicentric tracheids throughout the genus *Lycium* seems likely.

\*Stilbaceae: *Stilbe ericoides* L. (Martin 722, RSA) has vasicentric tracheids.

\***Stylobasiaceae:** \**Stylobasium australe* (Hook.) Prance (*Carlquist* 5227, 5434) has a moderate number of vasicentric tracheids; they are less common in *S. spathulatum* Desf. (*Carlquist* 4453).

**Thymeleaceae:** Metcalfe and Chalk (1950) state that “vessels of *Daphne*, *Dirca*, and *Ovidia* are mixed with a few vascular tracheids and some extremely small vessels.” Kanehira (1921) reported “tracheids” in *Wikstroemia indica* C. A. Mey. I interpret all of these as instances of vasicentric tracheid occurrence. To these, I can add *Dirca occidentalis* Gray (*Abrams* 1106, POM); \**Gnidia polystachya* Berg (*Carlquist* 15852, RSA); and \**Pimelea spectabilis* (Fisch.) Meyen (*Carlquist* 5939); some other collections of *Pimelea* from southwestern Australia appear to lack vasicentric tracheids.

\***Tremandraceae:** *Tremandra stelligera* R. Br. (*Carlquist* 5551, RSA) and *Platytheca juniperina* Domin (*Carlquist* 5688, RSA) have libriform fibers only, but in \**Platytheca verticillata* (*Carlquist* 6036, RSA), vascular tracheids are present. *Tetratheca retrorsa* (published as “*T. sp.*,” *Carlquist* 1977) and species of *Tetratheca* the wood of which was described by Heimsch (1942) have only tracheids (in basal caudexlike portions of the plant), suggesting that the condition in *Tetratheca* may be derived from one in which tracheids were present and in which libriform fibers are then lost.

\***Turneraceae:** \**Turnera ulmifolia* L. (*Metcalfe* 30011, UC) has vasicentric tracheids.

**Ulmaceae:** the sole clear report of vasicentric tracheids for this family is that of Braun (1970) for *Ulmus laevis* Pall. I can add a new report for \**Celtis reticulata* Torr. (*RSABG* 11583). The drawings (likely made from macerations) and photographs by Greguss (1959) for species of *Celtis*, *Ulmus*, and *Zelkova* almost certainly indicate presence of vasicentric tracheids in the species he studied.

\***Verbenaceae:** \**Lantana montividentis* Briq. (cult. LASCA) and \**Lippia wrightii* Gray (*RSABG* 11683) have vasicentric tracheids reminiscent of those in Lamiaceae.

\***Violaceae:** \**Hybanthus brevibrus* (Benth.) Domin (*Carlquist* 5748, RSA) and two other Australian species of *Hybanthus* (*Carlquist* 5170, 5298, RSA) from dry regions have vasicentric tracheids. They may also be reported in \**Agation deplanchei* Brogn. & Gris (*Carlquist* 15338, RSA), a climber from relatively dry lowland floras of New Caledonia, and \**Hymenanthera crassifolia* Hook. f. (cult. Orpet Park, Santa Barbara), a shrub from dry coastal regions of New Zealand.

**Zygophyllaceae:** Metcalfe and Chalk (1950) claim that in this family, vasicentric tracheids are “typically present, but not observed in *Porlieria*.” I can report them in \**Fagonia laevis* Standl. (*Tilforth* 417, RSA) and \**Larrea tridentata* (Sesse & Moc.) Cov. (*Bissing* 200, RSA). As in Myrtaceae, Proteaceae, and Santalaceae, they are similar to fiber-tracheids but with wider diameter and denser covering of bordered pits.

The above listing demonstrates clearly that not only are vasicentric tracheids characteristic of dryland shrubs and trees, they also tend to be found in related families, although obviously they must have originated separately in a number of phylads of dicotyledons. Notable with regard to relationship are the families

of Violales (Malesherbiaceae, Passifloraceae, Turneraceae, Violaceae), Geraniales (Erythroxylaceae, Geraniaceae, Linaceae, Malpighiaceae, Polygalaceae, Zygophyllaceae), and Berberidales (Berberidaceae, Papaveraceae, Ranunculaceae). Despite their polyphyletic origin in dicotyledons, vasicentric tracheids may prove useful as an indicator of relationship in some instances: they are widespread in some orders, but absent entirely in others. Species in which occasional vasicentric tracheids were observed have been omitted from the above listing, which thereby consists of instances in which appreciable numbers of these cells may be found. One might expect that incipient cases of evolution of vasicentric tracheids would exist, of course.

Vasicentric tracheids appear to play an important role in the wood of vining dicotyledons. An essay devoted to this topic is in preparation. These cells may also play a significant role in the wood of tropical alpine shrubs: they are present in Hawaiian alpine species of *Argyroxiphium*, *Dubautia*, *Exocarpus*, *Geranium*, *Santalum*, and *Tetramolopium* (true tracheids are present in *Vaccinium*).

Although the occurrence of true tracheids in certain groups from Mediterranean-type climates represents a phenomenon allied to occurrence of vasicentric tracheids and may seem obvious, groups with true tracheids should be cited. Not only are there woods in which true tracheids accompany vessels, as in *Adenostoma*, consideration should be given to woody gymnosperms, many of which occur in these regions. Some of these have true tracheids plus vessels (*Ephedra*) although most are vesselless. Attention should also be paid to woody monocotyledons on Mediterranean-type climates, such as *Yucca* or *Xanthorrhoea*, in which the secondary tissues of stems have xylem consisting wholly of tracheids.

Vasicentric tracheids have clearly increased in abundance in some groups with relation to evolution into progressively drier habitats. These cells are absent in many Oleaceae, Pittosporaceae, Rhamnaceae, and Violaceae, for example, but are present in dryland species of those families.

Further work is needed to establish the phylogenetic sequence by which vasicentric tracheids have originated in various groups of dicotyledons. Those phylads in which vasicentric tracheids seem to have originated by increasing abundance of vascular tracheids, so that tracheids spread into earlywood, obviously differ from those families in which vascular tracheids are very similar to fiber-tracheids in the same wood (e.g., Myrtaceae, Proteaceae). A further phylogenetic possibility is represented by those families in which vasicentric tracheids become increasingly abundant in wood (e.g., *Clematis*, *Passiflora*) so that some species have only vasicentric tracheids as the imperforate tracheary element type. I believe these instances are relatively infrequent and readily identified, and thus need not be confused with those numerous dicotyledons in which the background of imperforate tracheary elements in wood represents a phyletic retention of tracheids rather than a secondary acquisition of such cells. The interesting evolutionary significance of these quite disparate types of tracheid presence validates, in my opinion, the recognition of three types of tracheids instead of one, despite the greater terminological complexity. This situation is not unlike the recognition by Bailey (1936) of the term libriform fiber for the specialized end-product in tracheary element evolution. The term libriform fiber is generally recognized now, despite the need to use an additional term, extraxylary fiber, for cells of the same morphology but with a quite different phylogenetic and organographic origin.

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NOTE ADDED IN PROOF

An additional family can be added to the listing for vasicentric tracheids, *\*Bernardia incana* Wats. (*Stark 1642*, RSA) of *\*Euphorbiaceae*, a shrub of southern California; the figures in the abstract reflect this late addition. Vasicentric tracheids can also be reported for *\*Solanum xantii* Gray (*Wolf 3496*, RSA) of *Solanaceae*, also from southern California, and for two more *Asteraceae*: *\*Dimorphotheca cuneata* Less. of South Africa (see *Aliso 6[2]:1–23*, 1966) and *\*Inula viscosa* Ait. from Italy (see *Aliso 5:21–37*, 1961). In the southern California flora, two genera should be added to the list of woods bearing tracheids: *Polygala acanthoclada* Gray (*Polygalaceae*) and *Peraphyllum ramosissimum* Nutt. (*Rosaceae*). Note should be taken of the fact that many woods in which vessels occur in diagonal aggregations (also known as “dendritic patterns, arclike patterns,” etc.) have vasicentric tracheids; this grouping pattern may also occur in some woods lacking vasicentric tracheids, but it may prove to be a useful indicator nonetheless.